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An Introduction to Eelgrass (*Zostera marina* L.): The Persistent Ecosystem Engineer

Introduction à la zostère marine (*Zostera marina*) : ingénieur de l'écosystème longévif

Herb Vandermeulen

Department of Fisheries and Oceans, Maritimes Region
Population Ecology Division
Bedford Institute of Oceanography
P.O. Box 1006, 1 Challenger Drive
Dartmouth, Nova Scotia
B2Y 4A2

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ABSTRACT

Eelgrass (*Zostera marina* L.) is a persistent ecosystem engineer. *Zostera* meadows 'filter' the water column, stabilize sediment, and buffer shorelines. The meadows are important nearshore habitats, which are also sensitive to human disturbance.

In the absence of significant anthropogenic impacts, *Zostera* meadows are persistent, perennial habitat features. Eelgrass beds can be more than one thousand years old. Eelgrass will persist even in the face of deteriorating environmental conditions or cyclic disease events, and it can 'bounce back' if conditions improve. One of the mechanisms for persistence on a bay wide scale is dispersal (seeds and vegetative material) and expansion into new habitats.

RÉSUMÉ

La zostère marine (*Zostera marina* L.) est un ingénieur de l'écosystème longévif. Les herbiers de *Zostera* « filtrent » la colonne d'eau, stabilisent les sédiments et exercent un effet tampon sur les zones riveraines. Les habitats côtiers importants que représentent les herbiers sont cependant vulnérables aux perturbations anthropiques.

En l'absence d'impacts anthropiques importants, les herbiers de *Zostera*, espèce longévive et vivace, comblent des besoins en matière d'habitat. Les lits de zostère peuvent être âgés de plus de 1 000 ans. Même si les conditions environnementales se détériorent ou si des périodes cycliques de maladie surviennent, la zostère marine se maintiendra, car elle peut « rebondir » lorsque les conditions s'améliorent. La dispersion (des graines ou du matériel végétal) est l'un des mécanismes utilisés par l'espèce pour persister dans une baie, tout comme l'expansion dans de nouveaux habitats.

INTRODUCTION

Eelgrass (*Zostera marina* L.) is a vascular marine macrophyte found rooted in sandy or muddy sediments on temperate coastlines (Vandermeulen 2005). The Department of Fisheries and Oceans (DFO) has evaluated eelgrass as 'sensitive' habitat and addressed this sensitivity against finfish and shellfish aquaculture impacts (Vandermeulen 2005; Vandermeulen et al. 2006).

Vandermeulen (2005) provides a detailed assessment of eelgrass sensitivity to a variety of chemical, biological, and physical factors. A summary table of factors affecting eelgrass, with threshold levels, was provided in that publication and reproduced here as Table 1.

Table 1 provides some context for discussing *Zostera* biology. The threshold levels are provided as guidance and will likely change as new information becomes available. For example, Table 1 indicates that if *Z. marina* is buried by sediment to a depth ≥25% of the plant height, mortality will be greater than 50%. A recent review by Cabaço et al. (2008) on the impact of sediment burial on seagrasses confirms this sensitivity. They report that *Z. marina* will experience 50% mortality if buried with 4cm of sediment, and 100% mortality if buried in 12cm.

The light information provided in Table 1 can be compared to data in the more recent review by Moore and Short (2006). They indicate that the minimum light requirement for *Z. marina* is >15% of surface light at leaves, and photosynthetic saturation occurs at light levels >200 µmol photon m^{-2} s^{-1}.

Eelgrass is an important component of nearshore marine environments, with value in the detrital food web, as a direct food source, and as an ecosystem engineer. It is particularly important to stress that eelgrass does not provide these services in an ephemeral manner. Eelgrass beds persist over time unless anthropogenic stresses force them into decline.

EELGRASS AND THE DETRITAL FOOD WEB

The detrital food web is defined by the particulate matter that comprises its main carbon and energy source. The importance of seagrass detritus in marine food webs was recognized in the early 1900s (Klug 1980). *Zostera* fragments and particles (green, senescent, or dead) are rapidly utilized by a host of bacteria, fungi, and protozoans (Klug 1980). Eelgrass detritus can be an important source of material for the detrital food web both locally and by export to other ecosystems (Walker et al. 2001). *Zostera* wrack washed up on shore is also rapidly colonized and consumed (Jedrzejczak 2002).

EELGRASS AS A DIRECT FOOD SOURCE

Direct consumer utilization of seagrasses is less than 5% of annual production (Klug 1980). However, in Canada there is evidence of sea urchins occasionally consuming *Zostera*, and Canada Geese and other Brandts can be significant consumers (Vandermeulen 2005).

EELGRASS AS AN ECOSYSTEM ENGINEER

Ecosystem engineers are living organisms that physically change their environment (Berkenbusch and Rowden 2007). Eelgrass fulfills this role by 'filtering' the water column, stabilizing sediment, and buffering shorelines.

Eelgrass blades float vertically in the water column and act as baffles to water movement. Seagrass beds are known to attenuate wave energy and change the level of turbulence in the water (Koch and Verduin 2001). Flow reduction increases with the density of eelgrass beds (Vandermeulen 2005).

The net effect is a filtration of the water column as currents are slowed on a micro scale and sediment particles fall out of suspension. The process allows for sediment trapping and stabilization (Vandermeulen 2005). By promoting the deposition of suspended sediments, light availability can be enhanced (Koch and Verduin 2001).

The sediment trapping and stabilization process is also effective in reducing sediment transport (bed load). Seagrasses are known for their ability to stabilize coastal sediments (Klug 1980). Dense *Zostera* growing in low or moderate current regimes exhibits this influence quite strongly (Vandermeulen 2005).

Widdows et al. (2008) utilized a series of flume experiments to determine that high leaf densities of *Zostera* reduced near-bed flows and helped reduce sediment erosion. The effect was complicated by leaf height, sediment particle size, and the presence of microphytobenthos (sediment stabilization) versus herbivores (sediment disturbance and erosion).

On a local scale *Z. marina* stabilizes sediment as described above. When viewed on a larger scale, this action serves to buffer entire shorelines from erosion.

THE PERSISTENCE OF EELGRASS

Zostera in Time and Space

When identifying "Ecologically Significant Species" of the 'structure-providing' type, DFO does take into account the variability in abundance of that species over time (DFO 2006). Although *Z. marina* is a sensitive species with a relatively narrow niche as defined by its tolerance for various chemical, biological, and physical factors – the plants will persist over time.

Natural Cycles of Cover

The cover or abundance of eelgrass varies naturally over time. Ward et al. (1997) monitored fluctuations in *Z. marina* meadows in pristine Izembek Lagoon (Alaska), the largest known single stand of eelgrass in the world at approximately 16000ha in extent. Three sampling periods (1978, 1987, and 1995) indicated very similar spatial distribution of the beds and a slight net gain over the time period. Ward et al. (1997) concluded that the eelgrass beds had been stable over the 17 years of the study[1].

[1] The Izembek Lagoon eelgrass beds have been stable for at least 30 years (Short, pers. comm.).

As part of a study of eelgrass genetic structure, Rhode and Duffy (2004) used aerial photographs and ground monitoring records to identify 8 *Zostera* meadows in Chesapeake Bay with an age of at least 65 years. Some of these beds were over 100ha in size.

Orth et al. (2006a) studied the area just outside of Chesapeake Bay (Delmarva Peninsula). They provide coverage changes for eelgrass beds in 3 bays from 1986 to 2003, evidence for the persistence of the beds over that time.

Frederiksen et al. (2004a) examined long term changes in Danish eelgrass beds at 3 sites for the period 1954 to 1995/99 via a series of aerial photographs. The beds persisted over this time frame (approximately 45 years), but grew or shrank in a variable manner over time. Sediment movement at the more pristine exposed sites changed meadow patch shapes and landscape patterns over time, leading to a natural variation in cover of 50% or more between photographs (approximately 7 year intervals).

In an elegant study using genetic and growth data, Reusch et al. (1999) aged a single eelgrass bed in the Baltic. They estimated that the clone (covering 160 X 40m) could be 800 to 1600 years old. The Baltic has undergone major changes in ice cover, salinity, and temperature over this period.

Persistence When Stressed

Globally, seagrasses are in decline from a variety of anthropogenic stresses and much more effort is required to protect these very important nearshore primary producers (Orth et al. 2006b). From the examples cited above, it can be seen that naturally occurring beds of *Z. marina* will persist over time from decades to potentially hundreds of years[2]. However, an important question remains: "Do the beds persist over time and space when stressed?"

Keser et al. (2003) examined long term eelgrass declines in Long Island Sound from 1985 to 2000. They observed 5 separate die offs of eelgrass beds with no sign of recovery over the study period. Eutrophication was the suspected cause. Notably, eelgrass beds in study sites less likely to endure the effects of eutrophication experienced minor declines and persisted over the 15 year period.

The long term persistence of *Z. marina* in the face of coastal eutrophication was documented by Boström et al. (2002) for the Baltic Sea. A site studied in 1968-71 was revisited in 1993 (Tvärminne, Finland). No apparent change in biomass was seen, while some beds had an increase in shoot density. Surprisingly, *Zostera* was able to withstand purported eutrophication effects over this 25 year period and persist.

Harwell and Orth (2002) present maps of eelgrass distribution in Chesapeake Bay from the pre–1930s to the date of publication. Although many beds were lost over this time period due to the early 1930s wasting disease epidemic (more on that below), eutrophication, and increases in turbidity, a number of beds still persisted over this time period (over 70 years).

Ward et al. (2003) mapped eelgrass in Baja California comparing satellite images from 1987 and 2000. Over this time, submerged eelgrass area declined while intertidal beds expanded. Eelgrass losses were attributed to a winter flooding event which caused sediment loading and

[2] There is some information on long term persistence of Canadian eelgrass beds as well. The Manicouagan (Quebec) eelgrass beds have persisted for at least 20 years (Provencher, pers. comm.). Hooper (pers. comm.) has observed stable *Zostera* meadows over 40 years in Newfoundland.

turbidity, both of which are harmful to eelgrass (Vandermeulen 2005). Overall, the eelgrass beds persisted over the 13 year time span.

Similar decline of subtidal *Zostera* meadows due to water column turbidity is described by Bernard et al. (2007). In their study site (Berre Lagoon, southern France) *Z. marina* historically predominated in the lagoon[3], while *Zostera noltii* Hornemann (a smaller species found mainly in the shallows) took over later. They used aerial photographs from 1944, 1992, 1998, and 2004 to document the loss of deeper *Zostera* beds, the replacement of *Z. marina* by *Z. noltii*, and ultimately the near extinction of *Zostera* in the lagoon. A major shift in the lagoon ecosystem occurred in 1966 with the diversion of a river which caused major increases in freshwater and silt inputs. Later engineering efforts to reduce those impacts, along with reductions in urban and domestic pollution, did not cause *Zostera* to recover. It is important to note that *Zostera* did persist in the lagoon over this 60 year period, even with drastic changes to water column characteristics (primarily light reduction). Bernard et al. (2007) optimistically describe a slight drop in turbidity and a progression of *Z. noltii* in 2004.

Persistence in the Face of Wasting Disease

Godet et al. (2008) performed a mapping exercise involving old aerial photographs to determine recovery of French Atlantic coast eelgrass beds following their destruction in the 1930s by the wasting disease epidemic of the time[4]. In their analysis of air photos from 1924, 1953, 1982, 1992, and 2002 in the Chausey Archipelago, they determined that it took decades for the beds to recover from the disease event, and they have still not recovered completely. However, they report that eelgrass beds on the site are now rapidly expanding.

In an earlier publication, Jacobs (1979) examined the history of *Z. marina* in Roscoff, another site in northern France. Comparing maps from 1909, 1957, and 1976, Jacobs discovered a complete recovery from the wasting disease which struck this area in the 1930s, and an important recent expansion of the beds in the sublittoral. Similar to Godet et al. (2008), Jacobs (1979) describes an impressive record of site specific eelgrass persistence in northern France spanning approximately 70 years.

Den Hartog and Polderman (1975) studied eelgrass in the Dutch Waddenzee and noted persistence, but not complete recovery from the wasting disease event of the 1930s. They also described a decline from 1965 to the publication date likely due to cumulative effects of multiple anthropogenic stresses, eutrophication among them[5]. Their report is notable in that eelgrass distribution from 1869 to 1973 was recorded, a century of documented eelgrass persistence in the area. In their opinion:

> "For many centuries, probably since the formation of the Waddenzee, *Zostera marina* was widely distributed in the Dutch Waddenzee, both under sublittoral and eulittoral conditions." (Den Hartog and Polderman 1975).

[3] Evidence is presented for at least a century of *Zostera* presence.

[4] In the 1930s, eelgrass beds on both sides of the Atlantic were devastated by a fungal infection attributed to *Labyrinthula zosterae*.

[5] In a later evaluation of the Waddenzee (Wadden Sea) situation, Giesen et al. (1990) focus upon turbidity as a major factor in eelgrass decline. The turbidity increased in part from dyke construction and eutrophication. The turbidity hypothesis was still later corroborated by the in depth study of van derHeide et al. (2007).

The recovery of eelgrass beds in Denmark from the 1930s wasting disease epidemic by the 1960s was recorded by Frederiksen et al. (2004b). They conclude that deepwater eelgrass has declined in the last century due to eutrophication, while shallow water populations have been less effected and more persistent. Aerial photography evidence of 40 to 50 year persistence of eelgrass at 5 sites in Denmark was documented.

A more modern incidence of an outbreak of the wasting disease was reported by Short et al. (1986). They mapped eelgrass in the Great Bay Estuary (US east coast) in 1981 and 1984, documenting the loss of beds in the outer part of the estuary, due to *Labyrinthula* or another pathogenic organism. Those same maps indicate the persistence of the inner bay beds over the time period.

Persistence via Dispersal and Expansion into New Habitats

Verhagen and Nienhuis (1983) describe an interesting situation whereby an eelgrass bed expanded into an artificially created habitat. They studied Lake Grevelingen, a former estuary turned into a brackish lake via dam construction in 1971. The eelgrass in this body of water expanded in cover from a baseline in 1968 of 12km^2 to double or almost 4-fold increases in subsequent years. A total of 35km^2 were observed in 1981.

The Grevelingen lagoon situation was revisited by Nienhuis et al (1996). Using SCUBA, boat based observations and historical data, they created eelgrass cover maps for the period 1968 to 1993. They describe a dramatic decline in eelgrass cover beginning in 1985. By 1993, very few eelgrass beds were left. The potential cause of the decline during this latter period was related to man–made changes in the hydrodynamics of the lagoon and climate. The result was rapid water column nutrient depletion, low temperatures, and high salinity – all of which can have negative effects on the eelgrass.

The Grevelingen example illustrates an important point, given favourable environmental conditions, eelgrass will expand and colonise new areas. If those conditions are altered, the plants will respond.

One of the mechanisms for dispersal and subsequent colonization is seed production. *Z. marina* is a flowering plant. Its flowering shoots can be dislodged by wave action, and currents can disperse them for many 10s of kilometres (Erftemeijer et al. 2008). In this manner, eelgrass beds that have been damaged or lost entirely could be naturally recovered by seed sources over 100km distant (Erftemeijer et al. 2008). Reproductive fragments with viable seeds were found in wrack up to 34km from natural eelgrass beds by Harwell and Orth (2002).

Using microsatellite genetic markers, Reusch (2002) found that *Zostera* in shore wrack may not always come from local eelgrass beds. This also suggests dispersal via drift material.

PERSISTENCE OF OTHER SEAGRASSES

Z. marina is part of a larger family of seagrasses (about 60 species worldwide, Short et al. 2001). Gonzalez et al. (2008) studied caprellid abundance over 2 years in *Z. marina* and *Cymodocea* seagrass beds in southern Spain. The beds persisted over that time in biomass and cover, although the 1 study site with *Z. marina* did record a decline that was attributed to illegal bottom trawling fisheries.

Leriche et al. (2004) used maps from 1883 to 2000 to demonstrate the persistence of the seagrass *Posidonia oceanica* near Marseilles. In their analysis, they assessed the credibility of each map and some were rejected. Even so, there is a remarkable consistency in *Posidonia* cover in this century long time series, particularly between the 20 to 30m depth contours.

In a related study, Leriche et al. (2006) used aerial photographs and side scan sonar to record the shape of a 'relatively healthy' *P. oceanica* meadow in Bay of St.-Cyr (France) from 1955 to 2000. The limits of the bed changed little over this 45 year time frame.

SUMMARY

Zostera marina is important in detrital food webs and as wrack tossed on shore. In Canada, geese eat the plants directly. The plant also has structural importance in the nearshore, removing particles from the water column and stabilizing sediments.

Zostera marina is a very persistent, constant habitat feature. Under pristine conditions (e.g., Izembek Lagoon), eelgrass meadows can retain their shape and cover for decades. When stressed, shape and cover may vary over time, but the beds still persist.

Well documented studies demonstrate that eelgrass meadows will persist for decades. There is site specific evidence that eelgrass meadows can persist for a century or more. Individual *Zostera marina* meadows may even reach ages of over 1000 years (Reusch et al. 1999).

REFERENCES

Berkenbusch, K., and A.A. Rowden. 2007. An examination of the spatial and temporal generality of the influence of ecosystem engineers on the composition of associated assemblages. Aquatic Ecology 41: 129-147.

Bernard, G., C.F. Boudouresque, and P. Picon. 2007. Long term changes in *Zostera* meadows in the Berre lagoon (Provence, Mediterranean Sea). Estuarine, Coastal, and Shelf Science 73: 617-629.

Boström, C., E. Bonsdorff, P. Kangas, and A. Norkko. 2002. Long term changes of a brackish-water eelgrass (*Zostera marina* L.) community indicate effects of coastal eutrophication. Estuarine, Coastal, and Shelf Science 55: 795-804.

Cabaço, S., R. Santos, and C.M. Duarte. 2008. The impact of sediment burial and erosion on seagrasses: A review. Estuarine, Coastal, and Shelf Science 79: 354-366.

Den Hartog, C., and P.J.G. Polderman. 1975. Changes in the seagrass populations of the Dutsch Wadenzee. Aquatic Botany 1: 141-147.

DFO, 2006. Identification of Ecologically Significant Species and Community Properties. DFO Canadian Science Advisory Secretariat Science Advisory Report. 2006/041.

Erftemeijer, P.L.A., J.K.L. vanBeek, C.A. Ochieng, Z. Jager, and H.J. Los. 2008. Eelgrass seed dispersal via floating generative shoots in the Dutch Wadden Sea: A model approach. Marine Ecology Progress Series 358: 115-124.

Frederiksen, M., D. Krause-Jensen, M. Holmer, and J.S. Laursen. 2004a. Spatial and temporal variation in eelgrass (*Zostera marina*) landscapes: Influence of physical setting. Aquatic Botany 78: 147-165.

Frederiksen, M., D. Krause-Jensen, M. Holmer, and J.S. Laursen. 2004b. Long term changes in area distribution of eelgrass (*Zostera marina*) in Danish coastal waters. Aquatic Botany 78: 167-181.

Giesen, W.B.J.T., M.M. van Katwijk, and C. den Hartog. 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. Aquatic Botany 37: 71-85.

Godet, L., J. Fournier, M.M. van Katwijk, F. Olivier, P. Le Mao, and C. Retière. 2008. Before and after wasting disease in common eelgrass *Zostera marina* along the French Atlantic coasts: A general overview and first accurate mapping. Diseases of Aquatic Organisms 79: 249-255.

Gonzalez, A.R., J.M. Guerra-García, M.J. Maestre, A. Ruiz-Tabares, F. Espinosa, I. Gordillo, J.E. Sánchez-Moyano, and J.C. García-Gómez. 2008. Community structure of caprellids (Crustacea: Amphipoda: Caprellidae) on seagrasses from southern Spain. Helgoland Marine Research 62: 189-199.

Harwell, M.C., and R.J. Orth. 2002. Long-distance dispersal potential in a marine macrophyte. Ecology 83: 3319-3330.

Jacobs, R.P.W.M. 1979. Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. Aquatic Botany 7: 151-172.

Jedrzejczak, M.F. 2002. Stranded *Zostera marina* L. vs wrack fauna community interactions on a Baltic sandy beach (Hel, Poland): A short-term pilot study. Part II. Driftline effects of succession changes and colonization of beach fauna. Oceanologia 44(3): 367-387.

Keser, M., J.T. Swenarton, J.M. Vozarik, and J.F. Foertch. 2003. Decline in eelgrass (*Zostera marina* L.) in Long Island Sound near Millstone Point, Connecticut (USA) unrelated to thermal input. Journal of Sea Research 49: 11-26.

Klug, M.J. 1980. Detritus-decomposition relationships; pp. 225-245. In R.C. Phillips and C.P. McRoy [Editors]. Handbook of seagrass biology: An ecosystem perspective. Garland STPM Press, New York.

Koch, E.W., and J.J. Verduin. 2001. Measurements of physical parameters in seagrass habitats; pp. 325-344. In F.T. Short and R.G. Coles [Editors]. Global seagrass research methods. Elsevier Science, Amsterdam.

Leriche A., V. Pasqualini, C.F. Boudouresque, G. Bernard, P. Bonhomme, P. Clabaut, and J. Denis. 2006. Spatial, temporal, and structural variations of a *Posidonia oceanica* seagrass meadow facing human activities. Aquatic Botany 84: 287-293.

Leriche, A., C.F. Boudouresque, G. Bernard, P. Bonhomme, and J. Denis. 2004. A one-century suite of seagrass bed maps: Can we trust ancient maps? Estuarine, Coastal, and Shelf Science 59: 353-362.

Moore, K.A., and F.T. Short. 2006. *Zostera*: Biology, Ecology, and Management; pp. 361-386. In T. Larkum, R. Orth, and C. Duarte [Editors]. Seagrasses: Biology, ecology, and conservation. Springer, The Netherlands.

Nienhuis, P.H., B.H.H. De Bree, P.M.J. Herman, A.M.B. Holland, J.M. Vershuure, and E.G.J. Wessel. 1996. Twenty-five years of changes in the distribution and biomass of eelgrass, *Zostera marina*, in Grevelingen Lagoon, The Netherlands. Netherlands Journal of Aquatic Ecology 30: 107-117.

Orth, R.J., W.L. Luckenbach, S.R. Marion, K.A. Moore, and D.J. Wilcox. 2006a. Seagrass recovery in the Delmarva coastal bays, USA. Aquatic Botany 84: 26-36.

Orth, R.J., T.J.B. Carruthers, W.C. Dennison, C.M. Duarte, J.W. Fourqurean, K.L. Heck, Jr., A.R. Hughes, G.A. Kendrick, W.J. Kenworthy, S. Olyarnik, F.T. Short, M. Waycott, and S.L. Williams. 2006b. A global crisis for seagrass ecosystems. BioScience 56: 987-996.

Reusch, T.B.H. 2002. Microsatellites reveal high population connectivity in eelgrass (*Zostera marina*) in two contrasting coastal areas. Limnology and Oceanography 47: 78-85.

Reusch, T.B.H., C. Bostrom, W.T. Stam, and J.L. Olsen. 1999. An ancient eelgrass clone in the Baltic. Marine Ecology Progress Series 183: 301-304.

Rhode, J.M., and J.E. Duffy. 2004. Relationships between bed age, bed size, and genetic structure in Chesapeake Bay (Virginia, USA) eelgrass (*Zostera marina* L.). Conservation Genetics 5: 661-671.

Short, F.T., R.G. Coles, and C. Pergent-Martini. 2001. Global seagrass distribution; pp. 5-30. In F.T. Short and R.G. Coles [Editors]. Global seagrass research methods. Elsevier Science, Amsterdam.

Short, F.T., A.C. Mathieson, and J.I. Nelson. 1986. Recurrence of the eelgrass wasting disease at the border of New Hampshire and Maine, USA. Marine Ecology Progress Series 29: 89-92.

van derHeide, T., E.H. van Nes, G.W. Geerling, A.J.P. Smolders, T.J. Bouma., and M.J. van Katwijk. 2007. Positive feedbacks in seagrass ecosystems: Implications for success in conservation and restoration. Ecosystems 10: 1311-1322.

Vandermeulen, H. 2005. Assessing marine habitat sensitivity: A case study with eelgrass (*Zostera marina* L.) and kelps (*Laminaria, Macrocystis*). DFO Canadian Science Advisory Secretariat Research Document 2005/032.

Vandermeulen, H., G. Jamieson, and M. Ouellette. 2006. Shellfish aquaculture and marine habitat sensitivity case studies. DFO Canadian Science Advisory Secretariat Research Document 2006/036.

Verhagen J.H.G., and P.H. Nienhuis. 1983. A simulation model of production, seasonal changes in biomass and distribution of eelgrass (*Zostera marina*) in Lake Grevelingen. Marine Ecology Progress Series 10: 187-195.

Walker, D.I., G. Pergent, and S. Fazi. 2001. Seagrass decomposition; pp. 313-324. In F.T. Short and R.G. Coles [Editors]. Global seagrass research methods. Elsevier Science, Amsterdam.

Ward, D.H., C.J. Markon, and D.C. Douglas. 1997. Distribution and stability of eelgrass beds at Izembek Lagoon, Alaska. Aquatic Botany 58: 229-240.

Ward, D.H., A. Morton, T.L. Tibbitts, D.C. Douglas, and E. Carrera-Gonzalez. 2003. Long term change in eelgrass distribution at Bahia San Quintin, Baja California, Mexico, using satellite imagery. Estuaries 26: 1529-1539.

Widdows, J., N.D. Pope, M.D. Brinsley, H. Asmus, and R.M. Asmus. 2008. Effects of seagrass beds (*Zostera noltii* and *Z. marina*) on near-bed hydrodynamics and sediment resuspension. Marine Ecology Progress Series 358: 125-136.

Table 1. Factors affecting eelgrass, with threshold levels[6]

	Item	Threshold at which eelgrass beds may be damaged
Chemical Factors		
Nutrient loading	Water column nitrate	5 to 10 µM NO_3^- -N d^{-1} (*Zostera marina*)
	Pore water nitrate	20 mM (growth inhibition, *Z. marina*)
	Pore water sulphide	>70 µM H_2S (growth reduction, *Z. marina*)
	Pore water sulphide	>800 µM H_2S (photosynthesis reduced, *Z. marina*)
	Nutrient loading	30 kg N ha^{-1} yr^{-1} (loss of 80 to 96% of *Z. marina* bed area)
	Nutrient loading	≥60 kg N ha^{-1} y^{-1} (*Z. marina* beds gone)
	Macroalgal canopy	9 – 12 cm (decline in *Z. marina*)
	Enteromorpha mat	~4.5 kg wet wt m^{-2} (50% reduction in biomass, *Z. capricorni*)
Low oxygen	Water column [O_2]	<63 µM (*Z. marina* growth reduction)
	Water column [O_2] plus [H_2S]	<63 µM O_2 plus ≥ 100 µM H_2S (*Z. marina* photosynthesis shut down)
	Water column anoxia	A few days (*Z. marina* beds gone)
Biological Factors		
herbivory	Rissoidae	>30 individuals per shoot (*Z. marina* bed decline)
	Idotea	~100 individuals m^{-2} (*Z. marina* biomass loss)
	seed and seedling predation by invertebrates	no threshold available at present
bioturbation	*Dendraster excentricus*	~20 individuals m^{-2} (prevents colonization by *Z. marina*)
	Neotrypaea californiensis	100 individuals m^{-2} (prevents colonization by *Z. marina* and *Z. japonica*)
	Arenicola marina	68 individuals m^{-2} (*Z. noltii* buried)
	Hediste [*Nereis*]	400 – 700 individuals m^{-2} (excludes *Z. noltii*)

[6] Modified from Vandermeulen (2005) Assessing marine habitat sensitivity: a case study with eelgrass (*Zostera marina* L.) and kelps (*Laminaria, Macrocystis*).

	Item	Threshold at which eelgrass beds may be damaged
Introduced species	*Carcinus maenas*	≥4 individuals m^{-2} (*Z. marina*)
	Musculista senhousia	800 g dry mass m^{-2} (*Z. marina* rhizome inhibition)
	Codium fragile ssp. *tomentosoides*	no threshold available at present (*Z. marina*)
pathogens	*Labyrinthula zosterae*	>50% of leaf blade (*Z. marina* leaf production stops)
Physical Factors		
light[7,8]	% of surface light	<10% (*Z. marina*)
	µmol photons m^{-2} s^{-1}	<10 to 20 (*Z. marina*)
	No light	Several weeks (*Z. marina* beds gone)
Salinity and temperature	Salinity	>26 to 30‰ (*Z. marina*)
	Temperature	>25 to 30ºC (*Z. marina*)
Currents and scour	cm s^{-1}	<16 (*Z. marina* inhibition)
	cm s^{-1}	~ 25 (transition point for *Z. marina*)
	cm s^{-1}	>50 (inhibition of *Z. marina*)
	cm s^{-1}	>120 to 180 (max limit for *Z. marina*)
Sedimentation	depth of burial	≥25% of plant height (>50% mortality of *Z. marina*)

[7] Light calculations should add shading effect of epiphytes (i.e., take light measurement at true blade surface).
[8] Salinity, temperature and nutrient status will affect light compensation levels.